

THE MORPHOLOGY OF
TUBICAULIS AFRICANUS SP. NOV.
A FOSSIL FERN FROM TANGANYIKA

BY

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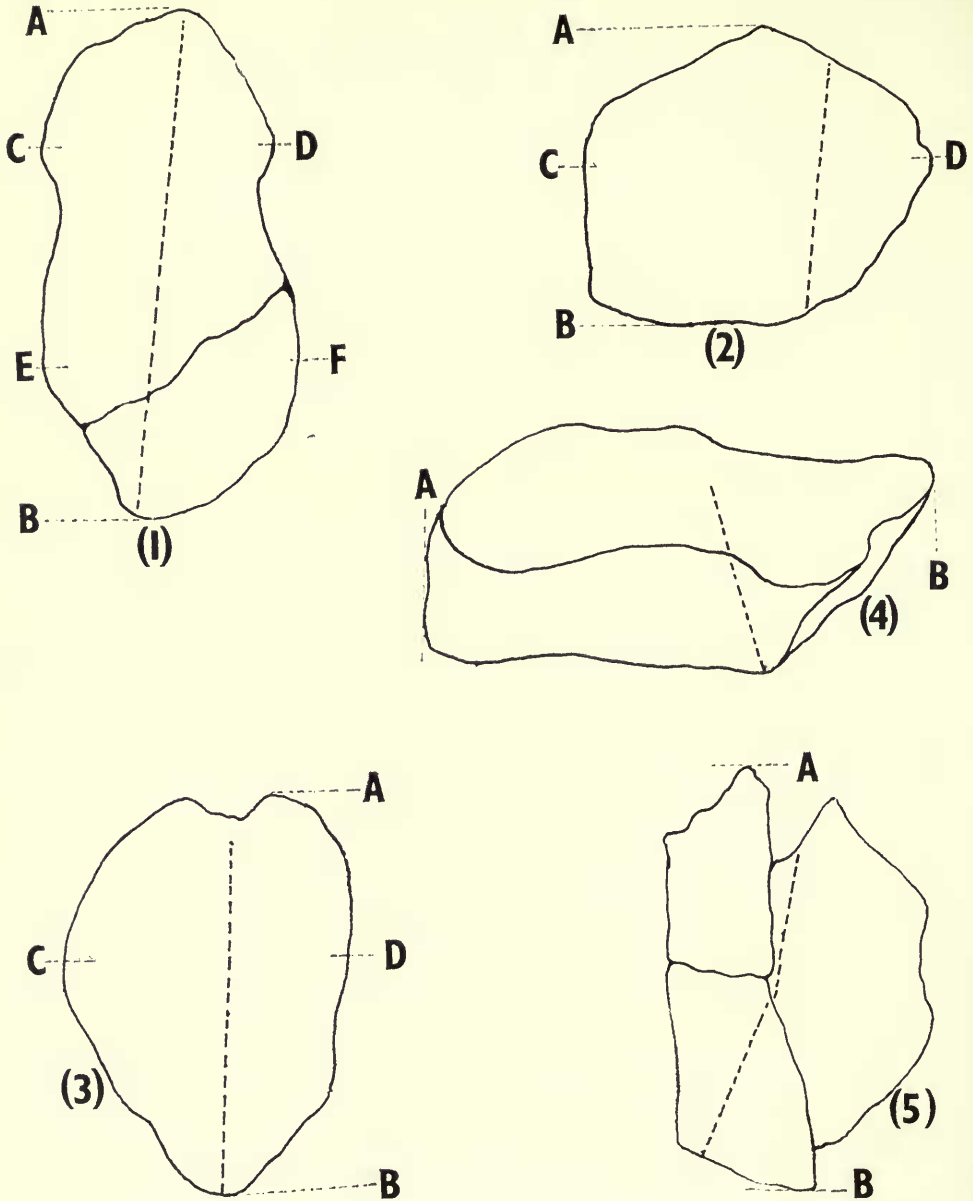
By HENRY SMITH HOLDEN & WILLIAM NOBLE CROFT

SYNOPSIS

The paper describes the morphology of a new species of fossil fern from the Ruhuhu area of Tanganyika. This is assigned to the genus *Tubicaulis* as *T. africanus* sp. nov. The relationships between the new species and the other fossil ferns assigned to the same genus and to possibly allied fossils are discussed.

INTRODUCTION

THE stratigraphy of the Ruhuhu area of south-western Tanganyika and its correlation with the Karroo formations of South Africa have been the subject of detailed study both by Stockley (1931, 1932, 1947) and Nowack (1937). Stockley's investigations resulted in the collection of numerous animal and plant fossils among which the silicified fern stems and their attached roots and leaf bases forming the subject of this study were included. They were discovered by Charles Kirchstein, who was at that time Stockley's Field Assistant, lying in a restricted area on the surface slope of an exposure of Upper Permian age. In this area there is a local disconformity between the Upper Permian strata and the scarp of the overlying Triassic Kingori Sandstones and, although it is possible that the specimens could have been dislodged from pockets in the sandstone, Stockley, who was consulted with regard to this possibility, regarded such derivation as improbable. Inevitably, there must be some doubt, however, as to whether the specimens are of Upper Permian or Lower Triassic age. They were sent, with other fossils, to the Department of Palaeontology of the Natural History Museum and a considerable amount of preliminary work on them was undertaken by the late W. N. Croft. The pressure of other duties and the increasing ill-health which ultimately led to his death resulted in their being put aside and they were not the subject of further study until the latter part of 1959 when Dr. E. I. White, Keeper of the Department, kindly made available both the specimens and Croft's notes. The specimens, five in number, had been given a common Locality Number, S559, and additional distinguishing letters A to E. They are now registered as V.44725-29 in the Department of Palaeontology. Croft made outline sketches of the specimens indicating their dimensions and these are reproduced as Text-figures 1-5. It will be seen from these that specimen V.44729 was broken into several pieces when received and that a deep crack was present on one face of specimen V.44725. Two of the specimens, V.44725 and V.44727, are illustrated in Pl. 33, figs. 1, 2 and it is clear from a surface examination of these and the other specimens that this fern possessed an upright stem which was surrounded



FIGS. 1-5. *Tubicaulis africanus* sp. n. Outline sketches of the five specimens as originally received indicating their dimensions. Fig. 1 is the holotype, Figs. 2-5 are the paratypes. The heavy broken line in each of the figures indicates the position of the stele. Not drawn to scale.

Fig. 1, Holotype, V.44725, A-B 20.2 cms., C-D 13.3 cms., E-F 13.2 cms.; Fig. 2, V.44726, A-B 9.3 cms., C-D 10.8 cms.; Fig. 3, V.44727, A-B 11.9 cms., C-D 9.7 cms.; Fig. 4, V.44728, A-B 16.5 cms.; Fig. 5, V.44729, A-B 11.5 cms.

by a thick armour of persistent leaf bases. Trial sections indicated that, as so frequently happens in silicified material, the quality of the preservation of the tissues varied considerably from one part of any given specimen to another and that the more delicate tissues of the fossil frequently were replaced, partly or wholly, by non-structural matrix. This replacement was notably the case in specimen V.44727. The plant tissues, when examined on a cut surface, were mostly light brown in colour and trial sections indicated that very little carbon had been preserved in them. Because of this, attempts to obtain "peels" by smoothing and subsequent etching with hydrofluoric acid often gave very unsatisfactory results, the action of the acid being uneven and resulting in the production of "ghost peels" in which either the structural details of the plant tissues were lost or some or all the tissues were missing completely. During the course of the investigation attempts were made also to obtain "peels" both of *Tubicaulis solenites* and *Grammatopteris baldaufi* for comparison with the new fern but etching with hydrofluoric acid proved equally unsuccessful with these also. An exception to the lack of success attending etching techniques was provided, however, by specimen V.44729 which yielded a number of good quality "peels". The information obtained from these was amplified by the examination of occasional successful "peels" from some of the other specimens together with ground sections and selected polished surfaces.

FILICALES

Family COENOPTERIDEAE

Genus *TUBICAULIS* Cotta, 1832: 15

Tubicaulis africanus sp. nov.

(Plates 33-36; Text-figs. I-II, 15, 16)

DIAGNOSIS. A fossil fern: stem upright surrounded by dense armour of persistent leaf bases: stem stele cylindrical, protostelic with numerous exarch protoxylem groups and with medulla of mixed tracheids and parenchyma: pitting of tracheids multiseriate scalariform or, in narrower tracheids, scalariform: cortex wide with scattered nests of sclerotic cells: petioles developed in close spiral succession: petiole traces initially monodesmic, later dividing into three, arched abaxially with free margins incurved when fully developed: region between stem and persistent leaf bases filled with long, uniseriate, septate hairs: roots with stout diarch stele arising at or near free margins of leaf traces.

HOLOTYPE. Specimen V.44725 in the Department of Palaeontology, British Museum, (Natural History).

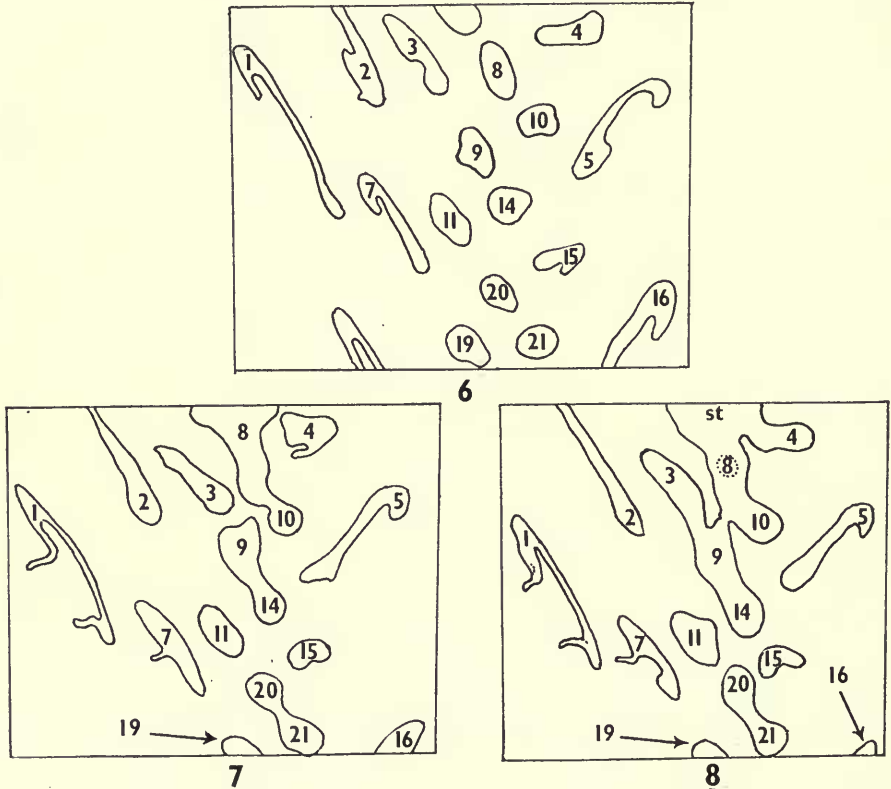
PARATYPES. Four specimens, V.44726-29, in the same Department.

LOCALITY. Ruhuhu area of south-western Tanganyika.

HORIZON. ? Upper Permian.

DESCRIPTION. *The Stem.* The surface tissues of the stem have not survived petrification and, as a consequence, it has proved impossible to determine its exact diameter but this ranges from approximately 4.5 cms. to 6.0 cms. Its centre is occupied by a small cylindrical stele which has a diameter of from 3.5 mm. to 4.0 mm. Its cylindrical character is somewhat obscured by the emission of a close

succession of spirally arranged leaf traces showing a complex divergence (Pl. 34, fig. 3; Pl. 36, fig. 1). The stelar protoxylem is exarch and consists of a number of separate groups of small tracheids distributed around the periphery of the stele (Pl. 34, fig. 3; Pl. 35, fig. 3). The majority of these possess scalariform pitting although, occasionally, they show suggestions of close spiral thickening. The metaxylem tracheids form a continuous hollow cylinder which varies somewhat in depth and



FIGS. 6-8. *Tubicaulis africanus* sp. n. Outline sketches of portions of three longitudinal "peels" from V.44729. Fig. 6 (Peel 11, V.44729(13)), Fig. 7 (Peel 13, V.44729(14)), Fig. 8 (Peel 14, V.44729(15)), showing the close succession of the petiole traces and the temporary vascular linkage of some of these. The petiole traces are numbered in the order of their emission from the stele.

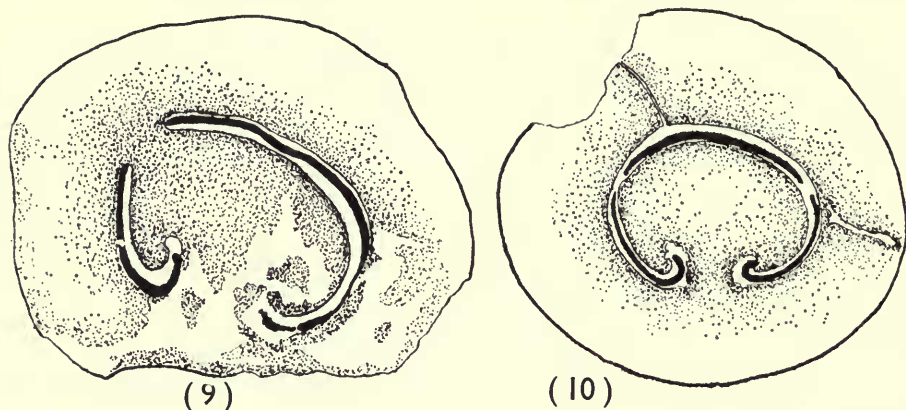
which encloses a "mixed pith" consisting of a parenchymatous ground mass among which tracheids are scattered singly or in small groups (Pl. 34, fig. 3; Pl. 35, figs. 1, 2). The medullary parenchyma is not sharply delimited from the main mass of the metaxylem but extends into it in the form of small groups or radial plates of cells which may penetrate locally almost to the outer margin of the stele and even into the bases of the departing leaf traces (Pl. 35, fig. 4). The type of pitting of the metaxylem is often difficult to determine owing to imperfect preservation but, where this is sufficiently good, it is seen to consist of a single row of trans-

versely elongated pits in the narrower tracheids whilst the wider ones possess two or three similar rows. The pitting is thus of the type termed multiseriate scalariform by Delevoryas & Morgan (1952). Most of the medullary tracheids are spindle shaped with pitting similar to that of the rest of the metaxylem although shorter tracheids with truncated ends are not uncommon, (Pl. 35, fig. 2). The phloem and its associated parenchyma have usually not been preserved and, at the best, are represented by shreds of pale brown tissue in which no structural features can be made out.

Scattered through the wide cortex are abundant groups of thick-walled cells forming sclerotic nests (Pl. 34, fig. 3; Pl. 35, fig. 1; Pl. 36, fig. 1), the component cells of which have dark contents. Some of these sclerotic nests have an attached fringe of parenchyma and are linked occasionally by similar groups of thin-walled cells. No continuous areas of parenchymatous ground tissue have been preserved although this does not appear to have led to any great spatial disturbance of the petiole and root traces traversing the stem cortex. The groups of sclerotic cells are frequently closely associated with these traces although this may be due, in part, to the loss of the cortical parenchyma.

The petiole. As already stated, the petiole traces are given off from the stem stele in close spiral succession and, as they begin to emerge from the outer tissues of the stem cortex, they produce in this an irregular series of superficial corrugations (Pl. 34, fig. 2). This crowded spiral succession may result also in a temporary vascular linkage between neighbouring petiole traces near the region of their emergence from the stem and is illustrated in Pl. 35, fig. 5 and, in outline, in Text-figs. 6-8. They develop a well-marked abaxial curvature immediately (Pl. 35, fig. 3) with the protoxylem tracheids forming a series of separate groups distributed along the convex adaxial surface. This distribution of the protoxylem is well shown not only in transverse sections of the petiole (Pl. 35, fig. 3) but also in tangential sections passing through the petiolar bundle at right angles to the sagittal plane immediately after it leaves the stem stele (Pl. 35, figs. 4, 5). Closely associated with each petiole trace is an oval mass of sclerotic cells which occupies its abaxial concavity. A continuation of this particular mass becomes closely applied to the abaxial face of the petiole trace as it moves outwards and forms a continuous strip along the whole abaxial face of the trace during its passage through the outer cortex of the stem. Similar groups of sclerotic cells are distributed also along the convex adaxial face of the trace and, near its point of origin, often form a more or less continuous band. Scattered irregularly through the strips of sclerotic cells which accompany the petiole traces are large ovoid cells which occur singly or in groups of two or three (Pl. 36, fig. 4). They are readily distinguished from the surrounding tissues by their larger size and by the absence of dark contents. They recall the elements described by C. Eg. & P. Bertrand (1911) as occurring in the inner cortex of *Tubicaulis berthieri* and which are interpreted by them as glandular cells. The petiole trace, during its passage outwards, takes a sharp upward course through the stem cortex. As it enters the base of the petiole, however, its upward curvature becomes much less pronounced so that, from the time of its inception to its later stages, the trace has the form of a sigmoid curve. During its transit,

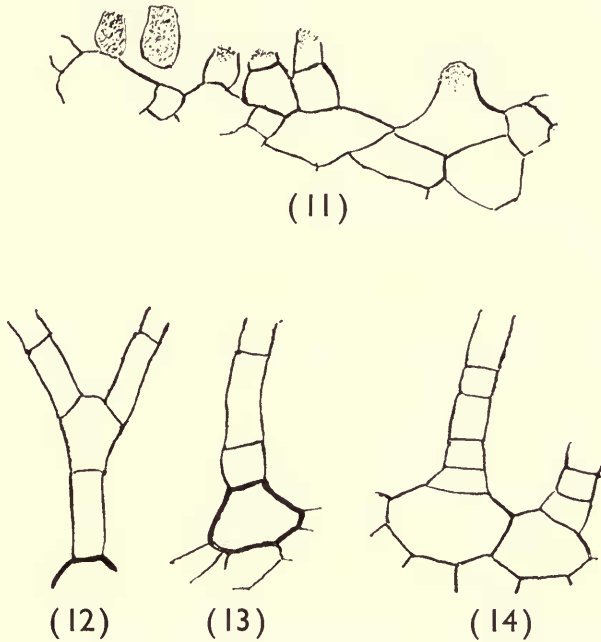
the abaxial curvature of the petiolar trace becomes steadily more pronounced with its free margins strongly recurved so that, when it enters the petiole, the xylem, in transverse section, has the shape of a slender letter C. (Pl. 36, fig. 1). The basal part of the petiolar cortex contains numerous scattered sclerotic nests and similar tissue, several cells in depth, forms a continuous layer immediately below the epidermis. This last, if preserved at all, is usually represented by a pale yellowish layer in which the cellular structure is lost. As the petiole moves further away from



FIGS. 9-10. *Tubicaulis africanus* sp. n. Camera lucida sketches of sections of two petioles. Fig. 9 from V.44726j shows, on the left, the complete division of the petiole trace and the separation of the distal part from the rest by cortical tissue and, on the right, the thinning of the xylem preparatory to division. Fig. 10 from V.44726k shows the symmetrical division of the petiole trace into three. Xylem in solid black, cortical tissues stippled (Both $\times 8$).

the stem, the sclerotic nests diminish in number and tend to disappear completely whilst the cortical tissues become homogeneous and are composed of small, somewhat thick-walled, cells apart from the continuous layer of sclerenchyma lying just below the epidermis. This stage appears to be reached only in the more distal parts of the persistent leaf bases. At the same level, extramarginal gaps are sometimes developed in the petiolar xylem. These gaps may occur initially on one side only or they may arise symmetrically on either flank of the trace (Text-figs. 9, 10). When the first examples of these gaps were found it was thought they might be artefacts which had resulted from locally imperfect petrification but further investigation showed that they were a normal feature in which the division of the xylem of the petiole trace was followed by its separation into three independent strands with the cortical tissues passing through the gaps between them. Whilst these gaps in the petiolar vascular supply resemble those resulting from the emission of extramarginal pinna-traces, it should be pointed out that none of the petioles examined shows any indication of the existence of such traces, although it is conceivable that they may develop from the contiguous margins of the xylem gaps or from the central bar at a higher level. However, no evidence of this has been found. A similar division of an initially monodesmic leaf trace is not uncommon in existing ferns (Davie, 1914),

typical examples being those of *Cibotium barometz* and *Saccoloma elegans*. Although the adaxially curved petiole trace in both these ferns is more elaborate than that of *Tubicaulis africanus* both show a transient division into three meristele, one median and two lateral, prior to their further sub-division (Bower, 1923; Davie, 1914; Gwynne-Vaughan, 1903). The persistent petiole bases are embedded in a dense mass of long uniseriate hairs through which the roots pass to the exterior (Pl. 36, fig. 3). Although the preservation of these hairs is imperfect, there are indications

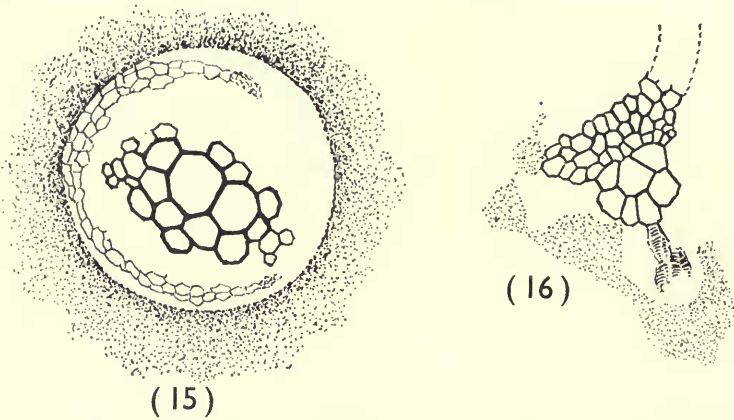


FIGS. 11-14. Fig. 11, *Tubicaulis africanus* sp. n. Portion of the petiolar epidermis showing the bases of several hairs, V.44726j. ($\times 300$). Figs. 12, 13, Bases of two hairs of *Cibotium regale* showing the thickened basal cell and, in 12, a bifurcation near the base ($\times 150$). Fig. 14, Bases of two hairs from *C. barometz* ($\times 150$).

that, like those found in many existing ferns, they were multicellular. Some of them arise from the basal parts of the petiolar epidermis and appear to develop from a single basal cell (Text-fig. 11) but it seems probable that many were developed also from the surface tissues of the stem. The existence of such surface hairs as distinct from flattened scales is widespread among palaeozoic ferns and they occur also in many existing ferns which are regarded as retaining other primitive characters (Bower, 1926). Comparatively short uniseriate hairs arising from a single basal cell form a thick covering to the rhizomes and petiole bases of *Matonia pectinata* (Seward, 1899). Those occurring in *Tubicaulis africanus*, however, are longer and appear to resemble more closely the long, brownish or golden yellow hairs which form a dense thatch clothing the stem apices and young petioles of various species of *Cibotium* such as *C. barometz* and *C. regale*. The hairs in these two species are

somewhat coarser than the ones present in *Tubicaulis africanus* although, like them, they arise from a single basal cell. (Text-figs. 12-14). In *Cibotium regale*, however, several examples have been noted in which the hairs divide into two equal branches near the base (Text-fig 12). The basal cell in this species has thicker walls than the remaining cells of which the hair is composed and, when the hair is shed, this basal cell persists as a large, convex, golden-yellow boss which stands out prominently from the smaller epidermal cells which surround it.

Roots. The roots arise on or near the free incurved margins of the petiole traces (Pl. 35, fig. 6; Text-fig. 16), usually in pairs, one from each margin. No evidence has been found indicating that they develop from the stem as well. As a rule, only the comparatively stout diarch stelar xylem of the root is preserved and this is surrounded by a sheath of dark sclerotic elements with a clear space between this



FIGS. 15, 16. *Tubicaulis africanus* sp. n. Fig. 15, T.S. of a root in the stem cortex showing the stout diarch stele and traces of the superficial tissues. The sclerotic tissue is stippled. V.44729(28). $\times 350$. Fig. 16, The recurved margin of a petiole trace showing the origin of a root. Note the larger diameter of the tracheids of the root metaxylem compared with those of the petiole. The sclerotic tissue is stippled. V.44729(27). $\times 200$.

and the root stele (Text-fig. 15). In this clear space but well separated from the stele, there are often traces of the other root tissues, these usually taking the form of a delicate complete or broken cylinder (Text-fig. 15). Occasionally, roots occur in which the whole of the cortical tissues have been partly petrified but, even here, the preservation is such that all that can be said is that they are parenchymatous. There is some evidence that the roots may branch whilst still within the stem cortex or among the hairs which enclose the persistent leaf bases. In a few instances, traces of the roots are found at the surface of the specimens and, where this is the case, these take the form of short oval rods or papillae representing the root steles.

DISCUSSION. The seven species at present included in the genus *Tubicaulis* comprise ferns showing wide differences in habit, these ranging from the relatively small epiphytic forms such as *T. berthieri* and *T. scandens* to those like *T. solenites*

and *T. africanus* which possessed stout upright stems enclosed in an armour of persistent leaf bases. This wide variation in habit is not, in itself, a valid reason for generic separation since a similarly wide variation in habit occurs in many existing fern genera. The genus *Asplenium*, for example, includes, in addition to both creeping and radially organised terrestrial species, minute epiphytes and massive specialised ones. They are included in the same genus by taxonomists in view of the agreement in their soral and sporangial characteristics. In the absence of the reproductive organs, however, palaeobotanists are compelled to rely solely on such morphological characters as are available in the specimens they study, this imposing a limitation which has been stressed already by Mamay (1952) and, more recently still, by Eggert (1959). A further handicap is often imposed by the small number of specimens which has been discovered and by their incomplete character, a handicap well-illustrated by *Tubicaulis* itself in which five of the seven species assigned to it have been described from single examples. In spite of these limitations, however, it seems reasonable, in the present state of our knowledge, to assign them provisionally to the same genus since all possess certain anatomical features in common, namely :

- (a) An essentially terete, protostelic axial vascular system devoid of secondary thickening with exarch protoxylem groups and in which the protostele may be wholly tracheidal or possess a core of mixed tracheids and parenchyma ;
- (b) petiole traces which depart from the stem stele, either as flat or slightly curved tangential bands which assume, ultimately, the shape of a letter C in transverse section and in which the curvature is abaxial, or in which the abaxial curvature is well-developed immediately on the separation of the petiole trace from the stem stele.

It will be noted that this definition of the essential generic vascular characteristics is slightly modified from that proposed by Mamay (1952) in the introduction to his description of *Tubicaulis scandens* and has been rendered necessary as a result of the discovery and description of other species subsequent to the publication of his paper.

The root systems of the various species provided no indications of common ancestry apart from the fact that the diarch steles are of the stout osmundaceous type rather than the slenderer type characteristic of existing leptosporangiate ferns. Like the roots of the fossil Osmundaceae, they show a wide variation in their source of origin (Kidston & Gwynne-Vaughan, 1907-14). Thus in *T. scandens* they arise solely from the stem (Mamay, 1952), in *T. sutcliffii* (Stopes, 1906), *T. multiscalariiformis* (Delevoryas & Morgan, 1952) and *T. stewartii* (Eggert, 1959) they arise from the stems and basal parts of the petioles and in *T. africanus* from the petioles only.

Adequate knowledge of the nature of the pinna-traces is lacking also. Stopes (1906) records the presence of two small strands in the cortex of one of the petioles of *T. sutcliffii* which were, presumably, pinna-traces although their origin could not be determined. Mamay (1952) shows that, in *T. scandens*, the pinna-traces are paired and that they are slightly but definitely extramarginal in origin whilst, in *T. solenites* in which they are also paired and slightly extramarginal, they bifurcate

whilst still within the petiolar cortex, each branch supplying a separate pinna (Stenzel, 1889, pl. 1, figs. 4-9). Morgan & Delevoryas (1954), on the basis of information supplied by Nickerson, state that in *T. multiscalariformis* the pinnae are borne in two rows, one on either side of the petiole. Grateful acknowledgments are due to Dr. Nickerson who has kindly supplied "peels" from coal balls in the collection of the Washington University Department of Botany confirming this.

A point worthy of note is that in both *T. solenites* and *T. scandens* the departure of the pinna-trace does not appear to cause a break in the continuity of the main petiolar strand. In attempting to indicate affinities within the genus, we are thus left only with the stelar characters and those of the petiole traces. Judged by these characters, the seven species assigned to *Tubicaulis* fall into two groups, *T. solenites*, *T. sutcliffii*, *T. berthieri* and *T. scandens* all possessing a homogeneous, wholly tracheidal proto-stele and a leaf trace which, initially, has the form of a flat or slightly curved tangentially expanded bar, whilst *T. multiscalariformis*, *T. stewartii* and *T. africanus* are characterized by the development of intrastelar parenchyma, slight in amount in *T. multiscalariformis* (Eggert, 1959) but much more abundant in both *T. stewartii* and *T. africanus*. These three species also agree in possessing petiole traces in which the assumption of an abaxial curvature occurs at a very early stage. Although there is a close resemblance in vascular structure between *T. stewartii* and *T. africanus* and also in the fact that both possess a surface covering of closely set uniseriate multicellular hairs, they differ considerably in habit and in numerous other features and these differences, combined with the wide difference in geological age, rule out any suggestion that they may have been specifically identical.

The relationship of the seven species now included in the genus *Tubicaulis* to other palaeozoic ferns does not appear to be a close one. The genera which resemble *Tubicaulis* in possessing an abaxially curved petiole trace are *Psalixylon* (Holden, 1960), *Apotropteris* and, possibly, *Anachoropteris* (Morgan & Delevoryas, 1954). All these are readily distinguished anatomically from *Tubicaulis* by their petiolar vascular characters and the likelihood of any close relationship either with that genus or with each other seems remote. A recent paper by Hall (1961) has described for the first time a radially organised plant bearing typical *Anachoropteris involuta* petioles. The stem of this plant is protostelic with, probably, exarch protoxylem. The stelar xylem is not homogeneous but contains plates of parenchyma interspersed among the tracheids. The trend towards the replacement of tracheids by parenchyma in the centre of the stele (i.e. towards medullation) is of wide occurrence in both the ferns and also in the fossil lycopods and there seems no valid reason why this plant should not be assigned to the genus *Anachoropteris* in view of its petiolar anatomy.

The fact that an abaxially curved leaf trace occurs in ferns along several apparently unrelated or very distantly related lines of descent suggests that this type of leaf trace may well have arisen independently from different ancestral stocks.

Of the other palaeozoic fern genera, *Grammatopteris* has been the one considered to be nearest *Tubicaulis* (Scott, 1920) although this view is open to some doubt. Of the two species of *Grammatopteris* of which both stem and petiole are known, *G. rigolloti* has been studied by Renault (1891, 1896) and Corsin (1937) whilst the

most recent investigation of *G. baldaufi* has been that of Sahni (1932). Both species possess an exarch protostele and, in both, the petiole trace has the form of a tangentially flattened bar which, in this respect, resembles that of those species of *Tubicaulis* in which the abaxial curvature of the petiole trace is, initially, slight or absent. Renault's account and figures of *Grammatopteris rigolloti* (Renault, 1891, 1896), although adequate for diagnostic purposes, left a number of features obscure and Corsin's more detailed study has served both to amplify Renault's account and to reveal additional points of interest. The most unexpected result of Corsin's work was that it demonstrated the presence in the holotype of a thin peripheral zone of secondary xylem surrounding the stem stele. This encloses a solid mass of primary xylem composed entirely of tracheids of varying diameter in which the pits apart from the protoxylem were multiseriate.

Renault's co-type was a small, thick preparation which showed no trace of secondary xylem. The tissues forming the core of the stele are imperfectly preserved but Corsin interpreted them as probably representing the pith, an interpretation which receives support from the two additional sections prepared from "le culot de taille" in which the presence of intrastelar parenchyma is undoubted. Corsin considered that the differences between the type section and the others were due to their being cut at different levels, the type being from nearer the base than the co-type and the additional sections (Corsin, 1937 : 52).

The petiole trace of *G. rigolloti*, although it shows a general resemblance to that of some species of *Tubicaulis* (e.g. *T. solenites*, *T. scandens*), differs in a number of details. Briefly, these are (a) that the protoxylem is confined to two slightly adaxial groups occupying the opposite margins of the trace, (b) that the slight curvature seen in the more distal parts of the trace is adaxial, and (c) that the pinna-traces are marginal in origin.

The specimens of *Grammatopteris baldaufi* do not appear to be so well preserved as those of *G. rigolloti* but it seems clear that the plant was also protostelic with a complete absence of intrastelar parenchyma but with a stellate core, most of which consisted of normal, elongated tracheids mixed with a small number of short, much wider ones (the "parenchymatous tracheids" of Sahni). The petiole trace is very like that of *G. rigolloti* with the protoxylem forming two groups, one at each end of the tangentially flattened xylem bar. The trace, in many instances, shows a slight adaxial curvature in the free petiole although this is possibly an artefact.

From the available data it seems clear that the relationship between *Tubicaulis* and *Grammatopteris* is not a particularly close one and that the genus *Tubicaulis*, as at present constituted, must continue to occupy a somewhat isolated position among the palaeozoic Filicales.

SUMMARY

Tubicaulis africanus is a fern probably of Upper Permian age which was discovered in the Ruhuhu area of Tanganyika. It possesses a stout, upright stem surrounded by a close armour of persistent leaf bases. The stem has a slender, cylindrical stele in which the protoxylem is exarch and in which the metaxylem consists of a peripheral, wholly tracheidal zone enclosing a core of mixed tracheids

and parenchyma. The wide cortex is characterized by abundant scattered nests of sclerotic cells with dark contents among which larger clear ovoid cells occur.

The petioles are given off in close spiral succession. The petiolar vascular supply is initially monodesmic with a distinct abaxial curvature which becomes steadily more pronounced distally and in which the free margins ultimately are recurved. The numerous protoxylem groups are distributed along the whole of the adaxial surface of the trace. The region between the surface of the stem and the petiole bases is packed with long uniseriate hairs.

The roots, which arise at and near the margins of the petiole traces, are diarch with a stout stele resembling that of the zygopterids and Osmundaceae.

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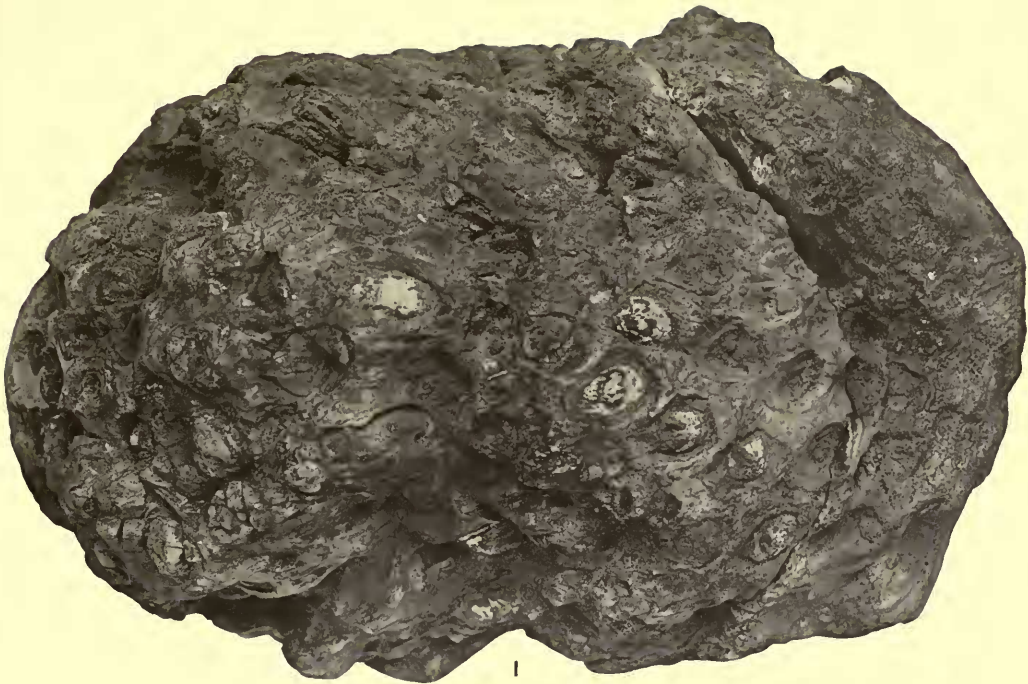


PLATE 33

Tubicaulis africanus sp. n.

FIG. 1. Holotype (V.44275). $\times \frac{2}{3}$ approx.

FIG. 2. Another specimen, V.44727, slightly enlarged.



1



6999

2

TUBICAULIS

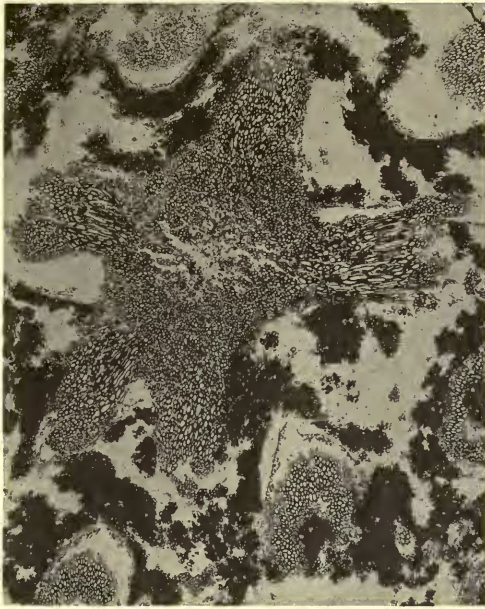
PLATE 34

Tubicaulis africanus sp. n.

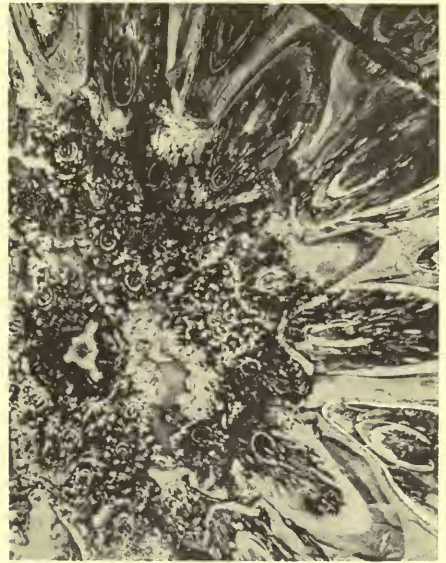
FIG. 1. Part of the smoothed and polished surface of a transverse section through V.44726a showing the armour of crowded, persistent leaf bases. About nat. size.

FIG. 2. Part of the smoothed and polished surface of a transverse section through V.44726c showing the stele and part of the stem cortex and leaf bases. ($\times 1.25$).

FIG. 3. T.S. of stele showing the "mixed pith" and five still attached leaf traces, V.44729 (28). ($\times 15$).



3



2



1

TUBICAILIS



PLATE 35

Tubicaulis africanus sp. n.

FIG. 1. L.S. of stele showing the "mixed pith", bases of leaf traces and patches of cortical sclerenchyma. V.44729(21). Longitudinal series No. 25. ($\times 15$).

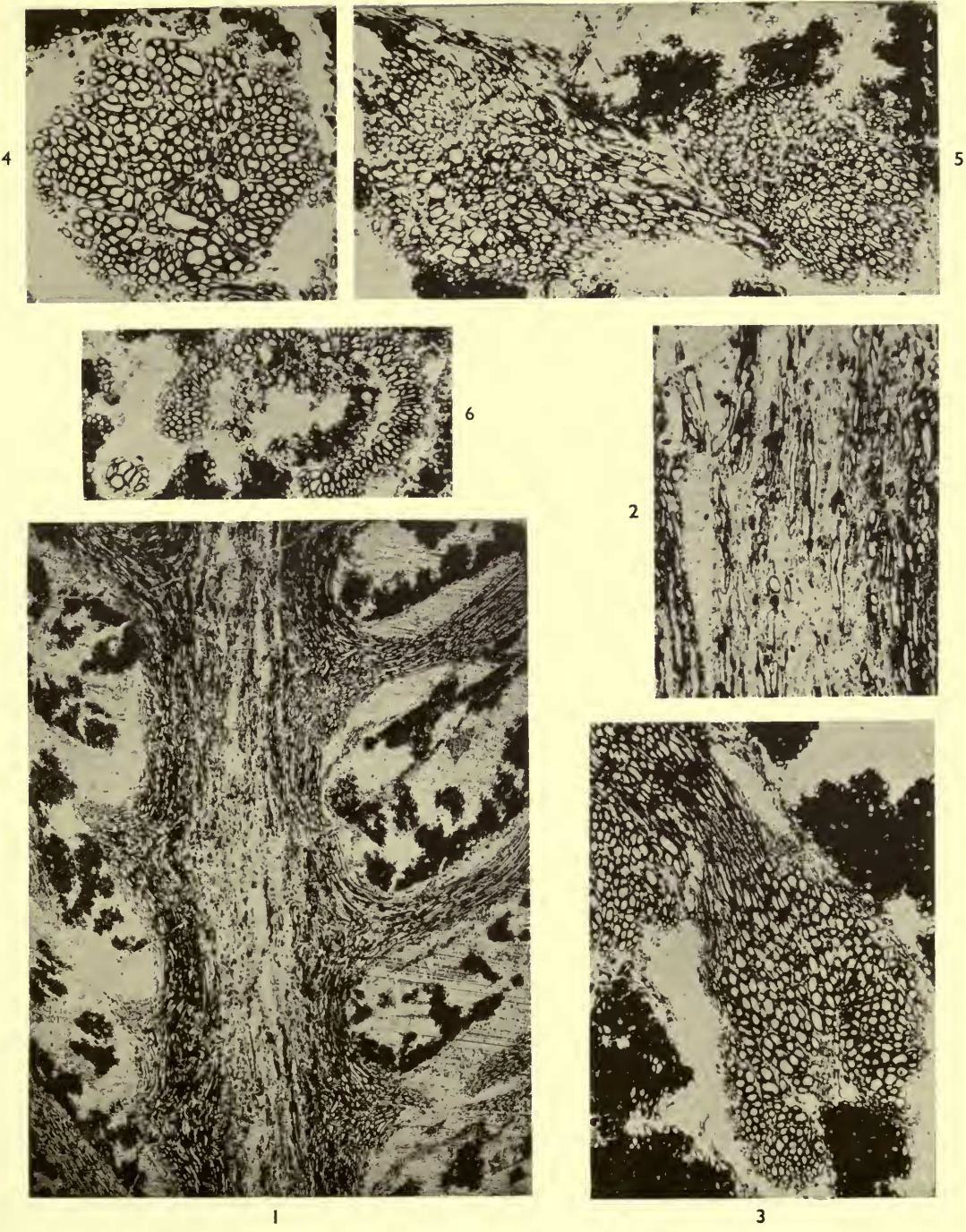
FIG. 2. L.S. of part of stele more highly magnified. V.44729(24). Longitudinal series No. 30. ($\times 30$).

FIG. 3. T.S. of a leaf trace at the point of departure from the stele, V.44729(25). ($\times 20$).

FIG. 4. Tangential section of a leaf trace showing the peripheral protoxylem groups, V.44729(13). ($\times 25$).

FIG. 5. Tangential section of two leaf traces showing their temporary vascular linkage, V.44729(14). ($\times 20$).

FIG. 6. T.S. of a leaf trace in the stem cortex from which a root trace has just been given off, V. 44729(25). ($\times 15$).



TUBICULIS

PLATE 36

Tubicaulis africanus sp. n.

FIG. 1. Tangential section through the stem cortex showing the crowded leaf traces and the scattered areas of sclerenchyma, V.44729(13). ($\times 30$).

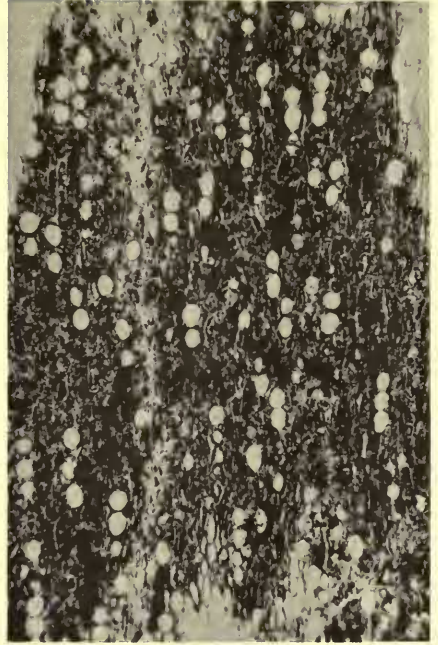
FIG. 2. T.S. of a fully developed leaf trace, V.44729(31). ($\times 12$).

FIG. 3. Part of the area between two petioles showing the packing of hairs, V.44726j. ($\times 30$).

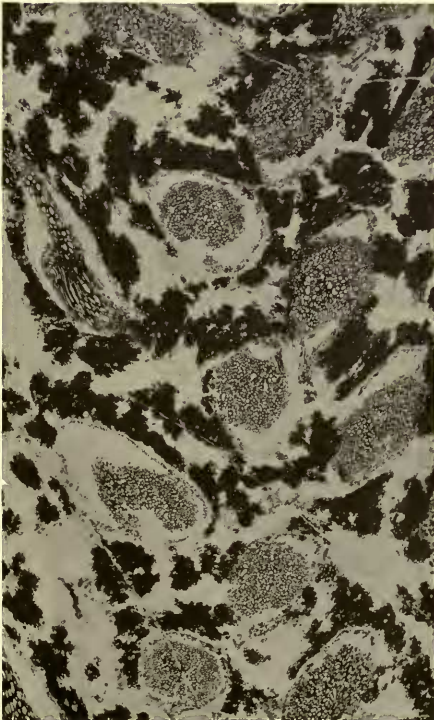
FIG. 4. An area of petiolar cortical sclerenchyma in L.S. showing the groups of "clear" cells, V.44729(30). ($\times 30$).



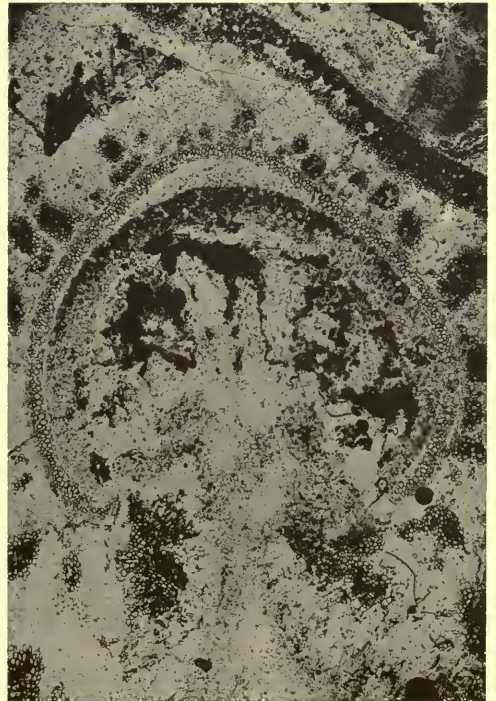
3



4



1



2

TUBICAULIS